

## RARE SPECIES AS EXAMPLES OF PLANT EVOLUTION

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ABSTRACT.— Rare species, including endangered ones, can be very valuable sources of information about evolutionary processes. They may be rare and valuable because: (1) they are evolutionary youngsters and could represent an entirely new evolutionary strategy of great scientific and practical value; (2) they are evolutionary relicts that have stored enormous amounts of genetic information of great worth; (3) they may represent endemic varieties that harbor a great deal of the genetic variability in the gene pool that would be of enormous value to a plant geneticist; the rarity of the plant is not necessarily correlated with the size of its gene pool; (4) they may represent unique ecological adaptations of great value to future generations. Studies of gene pools and the genetics of adaptation constitute a new and developing field of the future.

This morning I'm talking about a somewhat different topic than yesterday evening and one more in line with my usual interest because, as many of you know, I am primarily an evolutionist. The theme that I would like to develop is that rare species, including the endangered ones, can be very valuable sources of information about evolutionary processes. To illustrate that theme, I am going to give you examples of four alternative, but not mutually exclusive, theories that have been suggested for the reason that species are rare. One of the oldest, which was championed in the early part of the 20th century by J. C. Willis, was that the rare endemic species were youngsters. They appeared on the earth recently and haven't had time to spread. He wrote a whole book on the subject, which he called *Age and Area*. I first heard of that book from my systematics professor, M. L. Fernald, who was very much interested in rare species. He regarded them as senescent relicts, and strongly opposed Willis's theory. However, Willis was partly correct. We have perhaps more direct evidence of this than for any other hypotheses. This is expected, because the origin of some new species would be recent enough that we would know when it appeared. A now classic example is that presented by the late Marion Ownbey, of Washington State University, with respect to the goatsbeard genus, *Tragopogon*.

Projected on the screen is a chart which Ownbey put in the *American Journal of Botany* in 1950. The three species which are listed all have the chromosome number  $2n=12$ . They are well-known European plants introduced as weeds into North America. There are no species of *Tragopogon* in the Old World that have chromosome numbers higher than  $2n=12$  and  $n=6$ . However, in the backyards and railroad yards around Pullman, Washington, Ownbey found two different entities having 24 chromosomes, twice the number of all the others in the genus. By a series of ingenious hybridizations and analyses of chromosomes, he established without doubt that one of them, described as a new species, *T. miscellus*, was derived from hybridizations between *T. dubius* and *T. pratensis*. Its chromosome number has been doubled either before or after the initial hybridization, giving us a stable intermediate, a principle long known to geneticists. A second species, *T. mirus*, has originated in the same way from a cross between *T. porrifolius* and *T. dubius*. Because *T. dubius* did not exist in western North America before about the 1890s, the age of these two species when he first found them was not more than a half century. They now are spreading. They are known in one or two places in Montana. There is another locality in Arizona. They are certainly not endangered. A hundred years from now, they may have become com-

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mon weeds.

There are other very young examples, not quite so young as these. Indirect evidence suggests that some species have arisen since the retreat of the glacial ice from northern North America and the drying up of the climate in places like California where the Pleistocene was a rainy or pluvial period.

One example is that of three species in the genus *Layia*, or "tidy tips," an annual plant of the composite family, or Asteraceae. The three species involved are *L. jonesii*, *L. munzii*, and *L. leucopappa*. They are very closely related, on the border line of becoming species. They can be hybridized easily and the hybrid is partly fertile. They are more distantly related to *L. fremontii* and *L. platyglossa*.

Their distributions are as follows: *Layia jonesii* occurs near the coast of south central California, not far from San Luis Obispo; *Layia munzii* is found in the small valleys of the inner south coast ranges; and *L. leucopappa*, in the central valley of California, on one or two hillsides not far from Bakersfield. They are closely related entities occupying neighboring areas in the same general region. The climate of this region was drastically changed in the Pleistocene. It seems likely that the splitting of these three populations from each other is post-Pleistocene, about six to eight thousand years ago.

*Layia munzii* is on the border line of being rare in a dry season, but is certainly not endangered. *Layia jonesii*, being on the coast, might be endangered. *Layia leucopappa*, in the highly cultivated central valley, definitely is endangered. A nature conservancy group, located in Bakersfield, is very much interested in it. It occurs on a large private range area, the manager of which says they are going to preserve it for us. This is a case of a young species which is on the rare and endangered list.

Another example of a similar nature is a species of larkspur. *Delphinium hesperium* is a common widespread species of the oak woodlands in the inner coast ranges of California. *Delphinium recurvatum* is found in the central valley and bottom lands and *Delphinium gypsophilum*, as the name implies, lives in gypsumlike soil on the hills bordering the valley. It occupies a habitat between the

other two species. *Delphinium hesperium* and *D. recurvatum* have been crossed. The hybrid is partly fertile and looks like *D. gypsophilum*. The interesting thing is that when the F-1 hybrid is crossed with native *D. gypsophilum* it is found to be more compatible than the cross with either of its own parents. This is pretty good evidence that the native *D. gypsophilum* is derived from hybridization between the two other species. This again is a recent species. It is too common to be on the rare and endangered list, but it is certainly recent and uncommon relative to its ancestors.

An ancient species is the California Big Tree, *Sequoiadendron giganteum*. It is confined to certain groves in the Sierra Nevada in California, extending from Sequoia National Forest in the south in Tulare County into ever-smaller groves, to a very tiny one in the northernmost area in Placer County to the west of Lake Tahoe. It does not have a much-restricted gene pool. Horticulturists have found they can extract various modifications of it by simple inbreeding. Daniel Axelrod, with his brilliant studies of the paleobotany of western Nevada, has shown that California Big Tree was very abundant in Pliocene forests, six, seven, or eight million years ago in western Nevada when the Sierra Nevada didn't exist and the climate of Nevada, due to moist winds from the ocean, was still relatively mesic. Because of the Pleistocene changes in climate, it has become restricted in two ways: (1) the elimination of the stands to the east of the Sierra Nevada by aridity and (2) the reduction of the stands in California by the increasing length of the rainless dry summer. I say this because of research by the late Woodbridge Metcalf, extension forester at Berkeley. He showed that the big tree would seed itself only in a year when the dry season from May till October is shorter than usual. If it gets a few of these short dry seasons between seed germination and the time when the trees are 8-10 years old, then it competes with sugar pine, white fir, and other forest species. If young trees are exposed to a succession of normal dry summers, they cannot compete with the seedlings of the other species. This, then, is an example of an ancient species.

There are some others. One of the inter-

esting things that Professor Jack Major and I worked out some years ago is that the concentration of rare relictual species, which were more common in the past, is bipolar in California. It represents two elements, first a northwestern element which is related to the Pacific Northwest and Asia. The species involved are mainly trees or shrubs related to holarctic members of the same genera. Examples are the Weeping Spruce (*Picea breueriana*), which is narrowly restricted to this area. The Sadler Oak (*Quercus sadleriana*) is related to the Chestnut Oaks of the eastern United States, and is restricted to the Siskiyou Mountain area. The Port Orford Cypress (*Chamaecyparis lawsoniana*) is in this area. It contains several endemic species of mesic genera like *Vancouveria* and some genera of the saxifrage family.

In the southern area occur rare, endemic species like *Hesperocallis* of the Lily family, the jojoba shrub, *Simmondsia*, not particularly rare but certainly relictual.

By contrast, central California contains endemic species, which seem to be new like those of *Arctostaphylos* or *Manzanita*, already discussed, and other annuals. Because central California has received the greatest disturbance in relatively recent times, one can get some idea of whether a species is relictual or not, both by its taxonomic affinities and by the geographic areas in which it grows.

An example of an herbaceous species from the northern relictual area is *Darlingtonia californica*. It does not have official preservation that I know of in California. It should, because it is an attractive species, an insect-digesting pitcher plant. Every high school biology teacher wants one in the classroom, and people also like them in their homes. There is danger to them from vandalism. I sometimes blush when I go up the Oregon Coast Highway and see that Oregon has a preserved area of *Darlingtonia* labeled as such, while California doesn't.

The next group of rare and endangered species are of an entirely different nature. Here, I want to state publicly that one of my articles written in 1942, and often quoted, apparently is not correct. In 1942, I made the speculation that rare and restricted species would usually be so because of restricted gen-

etic diversity. At that time I was influenced by the work of Sewall Wright on inbreeding and its ramifications, which was very popular at that time. Now we have data on restricted species like *Clarkia franciscana*, which grows in only a single hillside in the city of San Francisco and which, as my colleague Leslie Gottlieb has shown, has as much biochemical variability in it in terms of enzyme alleles as *Clarkia rubicunda*, which is much more widespread throughout the San Francisco Peninsula. I now reduce the category of species that are rare because of restricted gene pool to a rather small one consisting of species that have not only become inbred because of small population size, but, in addition, because of the shift from cross-fertilization to self-fertilization or predominant fertilization. Again, Leslie Gottlieb has shown with his work on enzyme variability that in eastern Oregon there is a widespread species of the composite genus *Stephanomeria* (*Stephanomeria coronaria*), which has an enormous amount of genetic variability, but right next to it there is a very restricted species along Malheur Lake in eastern Oregon, *Stephanomeria malheurensis*, which has very little variability. One difference between the species is that *S. coronaria* is largely outcrossed and *S. malheurensis* is almost completely inbred. The inbreeding as much as the restriction in size of the population and habitat was responsible for the reduction in size of the gene pool. The same situation exists in some species of animals like the burrowing rodents of the Middle East, studied by several Israeli zoologists, and certain fishes in Mexican caves which have very restricted gene pools. One that is rather widespread, the southern alligator, apparently has extremely low variability in its gene pool. The whole hypothesis that there is a strong correlation between rarities and endangeredness and the size of the gene pool must be greatly modified, if not entirely rejected. In my own thinking, I am substituting the concept of ecological traps. Plant species may be hemmed in by environments that are so different from the ones in which they grow that they do not have the genetic potential to colonize those habitats. Sometimes the "traps" are quite clearly defined so that I call them ecological islands. Usually the soil

is so different on the islands, relative to that of the surrounding islands, that the plants are as if they were on an oceanic island surrounded by a sea of unfavorable soil conditions. Such an island is Pine Hill, 25 miles east of Sacramento. It consists of basic intrusives, a very distinctive type of rock, surrounded by the various metamorphic rocks commonly found in the Sierra Nevada foothills. Interestingly enough, this particular island is believed to have once been an oceanic island. Dr. Eldredge Moore of our geology department at Davis, in association with the new theory of Plate Tectonics, points out that basic intrusives are associated with the roots of volcanos. The situation could be explained if the rocks now exposed at Pine Hill were the roots of an ancient submarine volcano that arose in the Pacific Ocean to the west of what then was the seashore, but is now the eastern edge of the central valley. Because of crustal movements, this ancient island jammed itself against the older rocks.

A striking endemic on Pine Hill is *Femotodendron californicum* ssp. *decumbens*, a prostrate shrub that bears highly distinctive copper-colored flowers.

Another ecological island is in the area by Monterey and Pacific Grove. There are two species of rare endemic cypresses of the area. Neither of them is in danger now, because both are preserved. One is the well-known Monterey cypress (*Cupressus macrocarpa*), found only on the granite ledges near the shore. The other is the Gowen cypress, found only in the hard pan of the raised beach, in the interior of the peninsula.

Monterey pine is confined to the Monterey ecological island plus two others in California, one 50 miles north, the other 120 miles south. There is evidence that it is not restricted in its colonizing ability, if it has the right conditions, so that it could get out of its ecological trap. This is evident from what the Monterey pine has done in the southern hemisphere, in Chile, New Zealand, and Australia. In all three regions, extensive forests of this species have been planted that in many places look quite natural. Some trees are far taller than those in California, reaching heights of 100 to 150 feet.

Most interesting of all, in the vicinity of Canberra, Australia, I have seen Monterey

pine seedlings invading a forest of native *Eucalyptus*.

A well-known ecological island exists in the Sierra foothills of California, near the town of Ione. It is based on a hard pan soil which is of Eocene age, about 40 million years old. It was a sea-beach terrace facing the Pacific Ocean, which at that time covered all of the present central valley. It is dominated in many areas by an olive-colored shrub, *Arctostaphylos myrtifolia*, the Ione manzanita. There is a margin of the common gray manzanita, *Arctostaphylos viscida*, and interior live oak, but most of the area surrounding it is grassland consisting of introduced annual grasses and scattered blue oaks and digger pines that are the normal dominant vegetation of the area. The plants that are rare and endangered are held in check by the very special ecological conditions that prevail here. There is really an island within an island because a buckwheat, *Eriogonum apricum*, which is confined to the Ione manzanita island, grows only in the few most barren parts of it.

The gene pool of *E. apricum* is most interesting. There are three patches of it. The maximum distance from one to another is about 10 miles and there is one about halfway in between. Rod Myatt of UC Davis did a master's study on morphological variability and found that the different patches can be distinguished morphologically. They are races. There is not only a lot of variation within each of these patches, but distinctive differences between patches. In other words, it appears as if the Ione manzanita within its area of 10 miles has as much morphological variability as does another buckwheat, *Eriogonum nudum*, within an area of equal size, 10 miles in diameter in the Sierra foothills. The difference is that *Eriogonum nudum*, one of the most common buckwheats in California, has a multitude of races that are adapted to all sorts of climatic conditions over this extensive area. Another fact is that *E. nudum* is a much bigger species and its seeds are much bigger. Its seedlings are probably much more competitive so that it could colonize new areas more easily than could *Eriogonum apricum*. Perhaps *E. apricum* is a relic of the days when annuals, even native annuals, were much fewer than they are now.

It may have colonized the barren places that no other perennials could live in, when there wasn't so much annual competition. That's pure speculation. This again emphasizes the ecological entrapment which I believe is the basis for understanding the distribution of most of our rare and endangered species, independent of age and independent of quantitative sizes of gene pools.

The final example is similar. It is Convict Canyon in the eastern Sierra Nevadas. It is distinctive, because while most of the Sierra is either granitic or ancient acidic crystalline volcanics of Mesozoic age or earlier, Convict Canyon has a vein of limestone running through it. It is the only sizable part of the Sierra Nevada that has limestone in association with alpine or subalpine conditions.

Mount Baldwin, 12,000 feet high, supports a rare rock cress, *Draba nivalis*, and is the only locality in the Sierra Nevada. The nearest to it, as far as I know, are the Ruby Mountains in eastern Nevada.

One of the most remarkable plants, however, in this area, is a willow which is related to a Rocky Mountain species. *Salix brachycarpa*. Another species is a relative of the sedges, perhaps ancestral to the genus *Carex*. *Kobresia myosuroides* and an extremely localized dwarf bullrush, *Scirpus rolandii*, sometimes put in the species *Scirpus pumilus*, which has been the subject of interest for arctic alpine botanists for many years. The two discoverers of these species were Jack Major and Sam Bamberg.

Now, why do these rare plants grow here? It isn't because they are lime-loving calcophiles. The *Kobresia* grows on Mount Evans in Colorado which is acidic granite. Certainly *Scirpus rolandii* is to a certain extent a calcophile, but it doesn't seem as though the limestone is the basic reason. The other factor is this—limestone is porous. Because it holds water, on a steep slope like the one which supports the rare plants, water oozes out from the ground throughout the summer. Remember that the Sierra Nevada, in contrast to the Rocky Mountains or the Wasatch Range, has very few summer storms. They exist, but they're small and most of them hardly wet the ground. Much of the sierran area in the well-drained slopes becomes very dry in the summer, and the mesic plants have to grow where they get heavy snowfall during the winter. The rare plants, however, grow on a bench area that gets relatively less snow during the winter which is constantly coming out of the limestone formation. This, I believe is responsible for the unusual nature of the environment.

My final remark has become obvious from what I've had to say. Ecological genetics is a relatively new field. The combination between studies of gene pools and the genetics of adaptation, I predict, is a field which is just beginning to emerge and will be explosive in the next half century. Young scientists who are interested in native environments and wish to study them in depth from an analytical point of view will have an exciting career of discovery ahead of them.